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Estimation of Net Aerial Primary Production of Peltandra virginica (L) Kunth using Harvest and Tugging Techniques

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ESTIMATION OF NET AERIAL PRIMARY PRODUCTION OF _PELTANDRA VIRGINICA_ (L.) KUNTH USING HARVEST AND TAGGING TECHNIQUES

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APPROVAL SHEET

This thesis is submitted in partial fulfillment of
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ABSTRACT

Bimonthly measurements of individual tagged shoots in permanent plots and harvests of shoots in nearby plots were used to make four estimates of net annual aboveground primary production (NAAP) for Peltandra virginica. The tagging data were used to estimate production from the summation of mortality and the Allen curve. Peak biomass and Smalley (1958) estimates were made from harvest data. The four estimates were evaluated and compared. Life history characteristics including: recruitment, mortality, turnover, and life span were estimated from tagged shoot data.

The production estimates from the mortality (789.44 $g/m^2/yr$) and Allen curve (823.10 $g/m^2/yr$) methods were more than twice the peak biomass (352.64 $g/m^2/yr$) and Smalley (375.44 $g/m^2/yr$) method estimates. The two estimates from the tagged shoots incorporated seasonal recruitment, mortality, and turnover. These factors are especially important to include in estimating production for Peltandra, a fleshy tidal freshwater wetland plant with high turnover. Recruitment occurred throughout the season with a peak in May. Mortality occurred on all sampling dates with a peak in August. The mean life span was 53 days. Turnover was estimated from three methods NAAP/peak biomass (2.24), NAAP/mean biomass (6.83), and growing season/mean life span (3.6). Based on the findings of the life history patterns the mortality and Allen curve estimates represented true net production better than the harvest methods.

ESTIMATION OF NET AERIAL PRIMARY PRODUCTION OF *PELTANDRA VIRGINICA* (L.) KUNTH USING HARVEST AND TAGGING TECHNIQUES

INTRODUCTION

The purpose of this study is to make an accurate estimate of the net annual aboveground primary production (NAAP) for Peltandra virginica (L.) Kunth (Arrow Arum) by utilizing and comparing harvest and tagging techniques. Monthly harvest data were used to estimate production by the peak biomass and Smalley (1958) methods. Bimonthly tagging data were collected to estimate production from the summation of mortality and by using the Allen curve. The study also includes population parameters such as biomass turnover, mortality, recruitment, and life span from the tagged shoot study. There has been little previous work that concentrated on production dynamics of macrophytes in tidal freshwater wetlands. The production studies that concentrated on these wetlands often used harvest techniques more applicable to saltwater wetlands or grasslands hence a study specifically designed for tidal freshwater wetlands should be of benefit.

Tidal freshwater wetlands are located in the upper reaches of most of the Atlantic Coast's river systems; they comprise 500,000 to 1,000,000 ha along the Atlantic and Gulf Coasts (Odum et al., 1979). These areas are characterized by an average annual salinity of less than 0.5 ppt and by daily tidal exchange (Odum et al., 1984). Freshwater tidal wetlands are best described by the vegetation which is very diverse and may include, Wild Rice (Zizania aquatica), Peltandra, and spatterdock (Nuphar advena). In the mid-Atlantic and Georgia Bight regions, Odum et al. (1984) found 50 - 60 species at a single location. This distinguishes tidal freshwater wetlands from saltwater wetlands which are characterized by only a few dominant species. The vegetation in tidal freshwater wetlands also is characterized by high leaf mortality, fast decomposition rates, and a seasonal biomass turnover related to the seasonal sequence of dominant macrophytes (Odum et al., 1984). Primary production of macrophytes in these wetlands is equal to, if not greater than estuarine and saltwater wetlands at the same latitude (Whigham et al., 1978). Whigham et al. (1978) suggested that production in tidal freshwater wetlands may have been underestimated because few studies accounted for leaf mortality, plant turnover, belowground biomass, or herbivory.

Primary production from tidal freshwater wetlands supports trophic structures in the wetland itself and in adjacent uplands and water bodies (Odum et al., 1984). Mitch and Gosselink (1986) reported that the food chain is detritus based with benthic invertebrates serving as the link to organisims higher in the food web. Odum et al. (1984) reviewed the prinicipal components of tidal fresh wetlands and stated that they support a wide variety of terrestrial and aquatic species including insects, fish, reptiles, amphibians, waterfowl, and furbearers.

Tidal freshwater wetlands also have the potential to improve water quality. Grant and Patrick (1970) reported that these wetlands have considerable potential to assimilate nutrients through a combination of sediments, bacteria, algae, and vascular plants. Tidal freshwater wetlands lie at the transition zone of aquatic and terrestrial ecosystems, a strategic position for influencing the water quality of downstream estuaries. They have the potential for filtering pollutants, nutrients, and sediments in the water before it reaches the estuarine system (Simpson et al., 1983).

Accurate estimates of net annual primary production are necessary to characterize and model energy and nutrient dynamics in an ecosystem. Aerial primary production is usually estimated by harvesting vegetation throughout the growing season at regular intervals or at the assumed time of peak standing crop. Mason and Bryant (1975) suggested that serious errors may result if detailed energy and nutrient budgets are calculated using the peak standing crop as an estimate of production. Most harvest techniques underestimate production in salt and freshwater wetlands because they do not account for growth and leaf mortality between sampling periods (Hardisky and Reimold, 1977; Whigham et al., 1978; Shew et al., 1981). The greater the mortality and turnover the greater the underestimate (Bernard and Fitz, 1979). The underestimates may be significant when estimating production in a tidal fresh marsh where turnover and leaf mortality are high. De la Cruz (1978) suggested that information on mortality, natality, and phenology of plants or plant parts should be obtained from permanent sampling plots and incorporated in the productivity estimates from harvest techniques.

The emergent perennial _Peltandra_ _virginica_ (L.) Kunth, is an important primary producer in tidal freshwater wetlands. Few studies of wetland production have concentrated on this species. _Peltandra_ is a species in the family Araceae, and occurs along the East and Gulf coasts from southern Maine to northeast Texas and inland from Quebec to Mississippi (Robb, 1968). *Peltandra* is found in freshwater marshes and swamps and along the banks of ponds and rivers. The stem is a belowground vertical rhizome which branches and forms new plants separate from the parent plant. The new plants also form vertical rhizomes, resulting in a clustering of the plants (Goldberg, 1941).

Production for tidal freshwater wetlands has been underestimated because biomass turnover, belowground biomass, and herbivory have not been measured adequately (Whigham et al., 1978). The present study specifically addresses aboveground biomass production and turnover for *Peltandra*. The aboveground portion of production was studied because of its important interactions with the surrounding ecosystem and because seasonal production of belowground biomass is very difficult to measure with present technology.

Peltandra accounts for much of tidal freshwater wetland's production. It is found in mixed communities in the high marsh and in nearly monospecific stands in intertidal areas (Whigham et al., 1978). Doumlele (1981) found that *Peltandra* accounted for 53% of the community production in Sweet Hall Marsh, Virginia, the tidal freshwater site of this study. Most reported production estimates for *Peltandra* have been from the peak biomass and range from 67 - 1286 g/m^2 (Doumlele, 1981). These values represent underestimates of true net production because seasonal biomass turnover and mortality were not included (Whigham et al., 1978).

The objectives for this study are:

1. To make an accurate estimate of the NAAP for Peltandra.
2. To compare and evaluate four methods of estimating production for Peltandra. The four methods are: the peak biomass method, the Smalley method, the mortality method, and the Allen curve.
3. To describe several population parameters or life history characteristics of Peltandra which include production and mortality rates, shoot density, life span, recruitment, and turnover.

The peak biomass and Smalley methods estimate production from harvest data. The mortality and Allen curve use individually tagged shoot data. Peltandra has a high seasonal mortality (Pickett, 1984), so the mortality method was employed to measure the influence mortality has on the production estimate. Changes in recruitment and mortality are readily observed from the Allen curve.

LITERATURE REVIEW

Previous studies of tidal freshwater wetlands have significantly underestimated production (Whigham et al., 1978; McCormick and Somes 1982; and Odum et al., 1984). Methods for estimating primary production in these wetlands traditionally have employed various techniques of harvesting vegetation. The harvest techniques originally were developed for old upland fields and salt marshes which have different vegetation types and patterns than found in tidal fresh wetlands. These differences include composition changes in seasonal species, high species diversity, seasonal turnover of biomass due to leaf mortality, fast decomposition, and difficulty in measuring belowground biomass (Whigham et al., 1978; Odum et al., 1984).

The high turnover and fast decomposition rates are due in part to the chemical compositional differences between the plants in these ecosystems. Old fields and salt marshes are dominated by grasses that have more lignin and cellulose than the fleshy plants found in tidal fresh wetlands, such as _Peltandra_ which has a high nitrogen content and little refractive tissue (Odum and Heywood, 1978).

An example of seasonal species changes in a tidal freshwater marsh is seen along stream banks where _Nuphar luteum_ and _Peltandra_ dominate in the early spring while later in the summer _Amaranthus cannabinus_ and _Polygonum punctatum_ dominate (Whigham et al., 1978). Similarly, _Peltandra_ often dominates high marsh areas in the spring and then is replaced by a variety of other species later in the summer (Whigham et al., 1978). This is unlike saltwater wetlands which typically are composed of monospecific stands of grasses or rushes that show very little or no seasonal change in species composition and often have low turnover rates of one to two crops per year (Shew et al., 1981). Harvest techniques also underestimate NAAP in saltwater wetlands because they do not account for leaf mortality and growth between sampling intervals (Linthurst and Reimold, 1978). Following is a review of each method used in this study and a brief description of other methods used to estimate NAAP in wetlands.

Peak Biomass Method

The peak biomass method estimates NAAP from the greatest standing crop harvested during the year. Often only one harvest is done at the time of assumed peak biomass; this method assumes that the time of peak biomass is known, and in cases of only one harvest, is the same for all species. These are poor assumptions because climatic changes may change the time of peak biomass and species within an area may peak at different times of the year. Multiple harvests done on a regular interval throughout the growing season have also been used to determine the time of peak biomass for each species (Doumlele, 1981). Either method of determining peak standing crop is quick and inexpensive, but neither accounts for plant tissues that develop and die prior to or after sampling, or between monthly sampling intervals (Whigham et al., 1978). This leads to underestimates of NAAP in tidal fresh wetlands where turnover and leaf mortality are high.

Smalley Method

From monthly harvests, Smalley (1958) summed the positive changes in live and dead material between sampling intervals to estimate NAAP in a saltwater wetland. For a negative sum, production was assumed to be zero. This method is frequently used to estimate production in a variety of wetlands, and attempts to account for mortality between sampling intervals by collecting the dead material. It has been documented that the Smalley method underestimates NAAP in salt and freshwater wetlands because it does not account for all plant material that dies between sampling intervals, and it does not account for decomposition (Turner, 1976; Linthurst and Reimold, 1978; Whigham et al., 1978; and Shew, et al., 1981).

Other Multiple Harvest Methods

A variety of harvest techniques have been developed in many ecosystems such as in an old field by Wiegert and Evans (1964) and in grasslands by Lomnicki et al. (1968), and Milner and Hughes (1968). Wiegert and Evans (1964) accounted for production, mortality, and decomposition by harvesting paired plots. Wiegert and Evans calculated an instantaneous rate of disappearance of dead material from the paired plots by initially harvesting live material from both plots and the dead material from only one plot. Lomnicki et al. (1968) modified the Wiegert and Evans method by measuring mortality directly and based production calculations on growth of green material and production of dead material. This method, therefore, precludes the need to calculate the instantaneous rate of disappearance of dead material. Milner and Hughes's (1968) method summed positive changes in live material through sampling intervals over one year. This method did not account for dead material or decomposition.

These multiple harvest techniques have been applied to salt and freshwater wetlands and were reviewed by Turner (1976), Linthurst and Reimold (1978), Whigham et al. (1978), Shew et al. (1981), and Dickerman et al. (1986). These techniques include some factors of mortality and decompostion, however, all plant material that dies and decomposes between harvests cannot be accounted for (Whigham et al., 1978). Turner (1976) reviewed estimates of production in salt marshes and found they were underestimates because turnover of biomass between intervals was not adequately measured. Linthurst and Reimold (1978) and Shew et al. (1981) compared five harvest methods of estimating production in estuarine wetlands and found that all but Wiegert and Evans's method underestimated NAAP. They reported that Wiegert and Evans's method overestimated production because of the alterations made in the sample plots. Dickerman et al. (1986) reported that Wiegert and Evans's and Lomnicki's methods overestimated production because they altered the microenvironment. Dickerman et al. also suggest that Wiegert and Evans's method should not be used in tidal systems where litter is moved by tides. The above methods of determining mortality are dependent on harvesting dead material, which is very difficult to do with Peltandra because of its fast decomposition rate (Odum and Heywood, 1978).

Mortality Methods

To account accurately for mortality and production in wetlands between sampling intervals, measurements of individual plants and plant parts have been used to get a better estimate of production in numerous ecosystems. These studies included measurements of recruitment, growth, mortality, and turnover of leaf biomass from individually tagged shoots that were monitored during the growing season. In a tidal freshwater wetland Whigham et al. (1978) found that over a 55 day tagging period mortality among species was high and that production may increase twofold when adjusted for mortality during the growing season. Also in a tidal fresh wetland, Pickett (1984) reported a production estimate including mortality that was 2 to 3 times greater than the peak biomass. Pickett (1984) further reported a rapid biomass turnover from tagged Peltandra shoots.

In freshwater wetlands, Smith and Kadlec (1985) reported best production estimates by incorporating losses of tagged shoots between each sampling interval into production estimates based on peak standing crops in exclosures (cages). For a Typha latifolia stand, Dickerman et al. (1986) designed the "summed shoot maximum" method, a summation of the maximum masses of all tagged shoots and corrected for mean leaf turnover. Dickerman et al. compared harvest and tagging methods to estimate NAAP for Typha latifolia and found that the "summed shoot maximum" method resulted in a NAAP of 18 to 38% greater than the harvest estimates. They propose that early shoot mortality, leaf turnover and losses of portions of individual leaves are the causes for these underestimates.

In sedge wetlands Bernard and Gorham (1978) documented that the life history of shoots, especially mortality, had a significant influence on production processes and must be considered to get an accurate estimate of production. Tagging studies in sedge wetlands accounting for mortality resulted in a twofold increase in the production estimates (Bernard and MacDonald, 1973; Bernard and Hankinson, 1979).

Similarly, in salt marshes when seasonal mortality was accounted for production estimates increased. Leaf abscission from live *Spartina alterniflora* culms accounted for 31% of the annual production (Hardiskey, 1980). Mortality of tillers and leaves of *S. alterniflora* added 32% to the production estimate, harvest estimates in the same study were 12 to 27% lower than the estimate including mortality (Houghton, 1985). Reidenbaugh (1983) measured new production of tillers and culms and losses from leaves and culms which resulted in a much larger production estimate for *S. alterniflora* than previously had been reported for that region.

Allen Curve Method

The Allen curve, a method of demographic analysis developed for estimating fish production by following the life cycle of tagged cohorts (Allen, 1951) has been applied to plant populations (Mathews and Westlake, 1969; Mason and Bryant, 1975; and Dickerman et al., 1986).

Allen (1951) designed this method to estimate production of fish populations with very high mortality. It estimates cohort production graphically by relating cohort shoot density and the mean cohort biomass per shoot over the growing season (Dickerman et al., 1986). The total area beneath the curve is proportional to production. The method assumes that all shoots in one cohort have the same weight. Using the Allen curve method Mathews and Westlake found a production estimate 2.2 times greater than the peak biomass in a _Glyceria maxima_ population. In a _Typha angustifolia_ stand Mason and Bryant (1975) used the Allen curve to estimate production which resulted in a 23 to 28% greater estimate than the peak biomass. Dickerman et al. reported a production estimate for _Typha latifolia_ using the Allen curve that was 1.2 to 1.6 times greater than the peak biomass.

Turnover

Longevity is a major controlling factor of turnover rate because as the former increases, the latter must decrease (Odum, 1971). Therefore, a productivity value can be obtained from a turnover rate based on longevity (Shew et al., 1981). Turnover traditionally has been calculated as the ratio of production to peak or to mean biomass (Gosselink et al., 1977; Gallagher et al., 1980). An "experimental turnover rate" based on longevity and independent of any production estimate can be used to judge production estimates and their respective turnover rates (Shew et al., 1981). Production of _Juncus roemerianus_ was 2.3 times greater than the mean biomass when measurements of growth rate and leaf longevity were included in the production estimate (Williams and Murdoch, 1972).

Summary

It has been documented that the peak biomass and Smalley methods underestimate production in salt and tidal fresh wetlands (Whigham et al., 1978; Shew et al., 1981). These methods were used in this study to compare with the other two tagging estimates of production used in this study, and with other studies that typically employ harvest methods. The mortality method used in this study was similar to the summed shoot maximum method proposed by Dickerman et al. (1986), however, there were two differences between the methods. One difference was that no correction was made for mean leaf turnover because the shoots of *Peltandra* have only one leaf. The other difference was that to get mortality rates, maximum weights reached by the shoots were recorded as lost on the date of death. The Allen curve was the fourth method used in this study to estimate production.

MATERIALS AND METHODS

Study Site

The study was conducted in Sweet Hall Marsh, located 19 km from the mouth of the Pamunkey River, a tributary of the York River, Virginia (Figure 1). Based on the dominance of tidal freshwater wetland vegetation, an annual salinity range (0.0 - 5.0 ppt), and a tidal range (1 meter) the marsh is considered a tidal freshwater wetland. The marsh consists of 444 ha of wetlands, including 29 ha of wooded swamp (Doumlele, 1981).

The sampling area (Figure 2) is located on a small peninsula bordered by the Pamunkey on one side and by a creek, approximately 25 meters wide, that runs through the marsh. To sample representative areas of _Peltandra_ two transects were chosen for sampling, one along the river and the other along the entrance of a creek adjacent to the river plots, the mean elevations above mean sea level were 0.71 and 0.96 meters, respectively. The river transect was wider and had a gentler slope than the creek transect. Both transects ran parallel to the water in the mid-intertidal zone of a monospecific stand of _Peltandra_. A monospecific stand was chosen to minimize the effects of seasonal species compositional changes.

Figure 1. Chesapeake Bay with inset of study site Sweet Hall Marsh, Virginia.

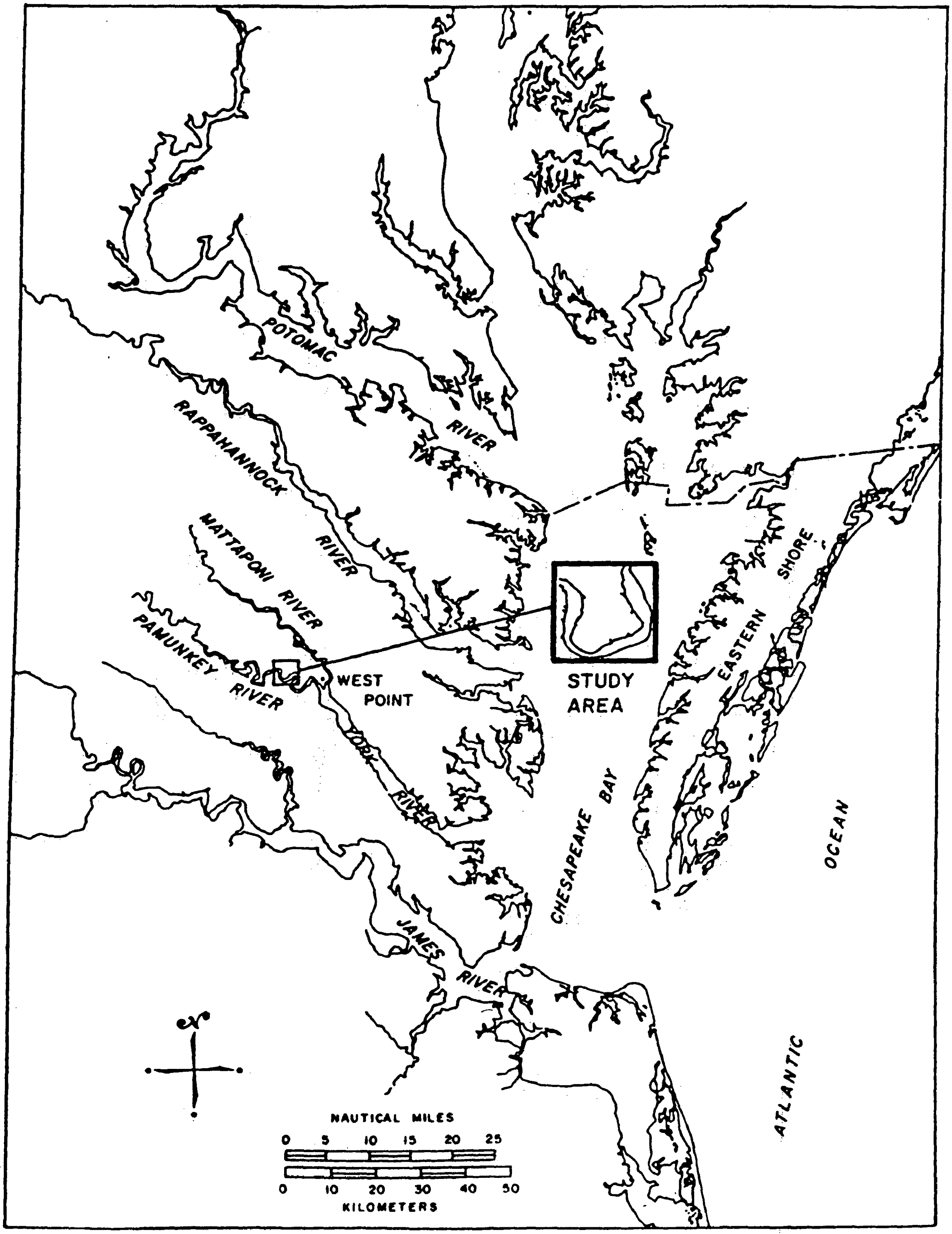
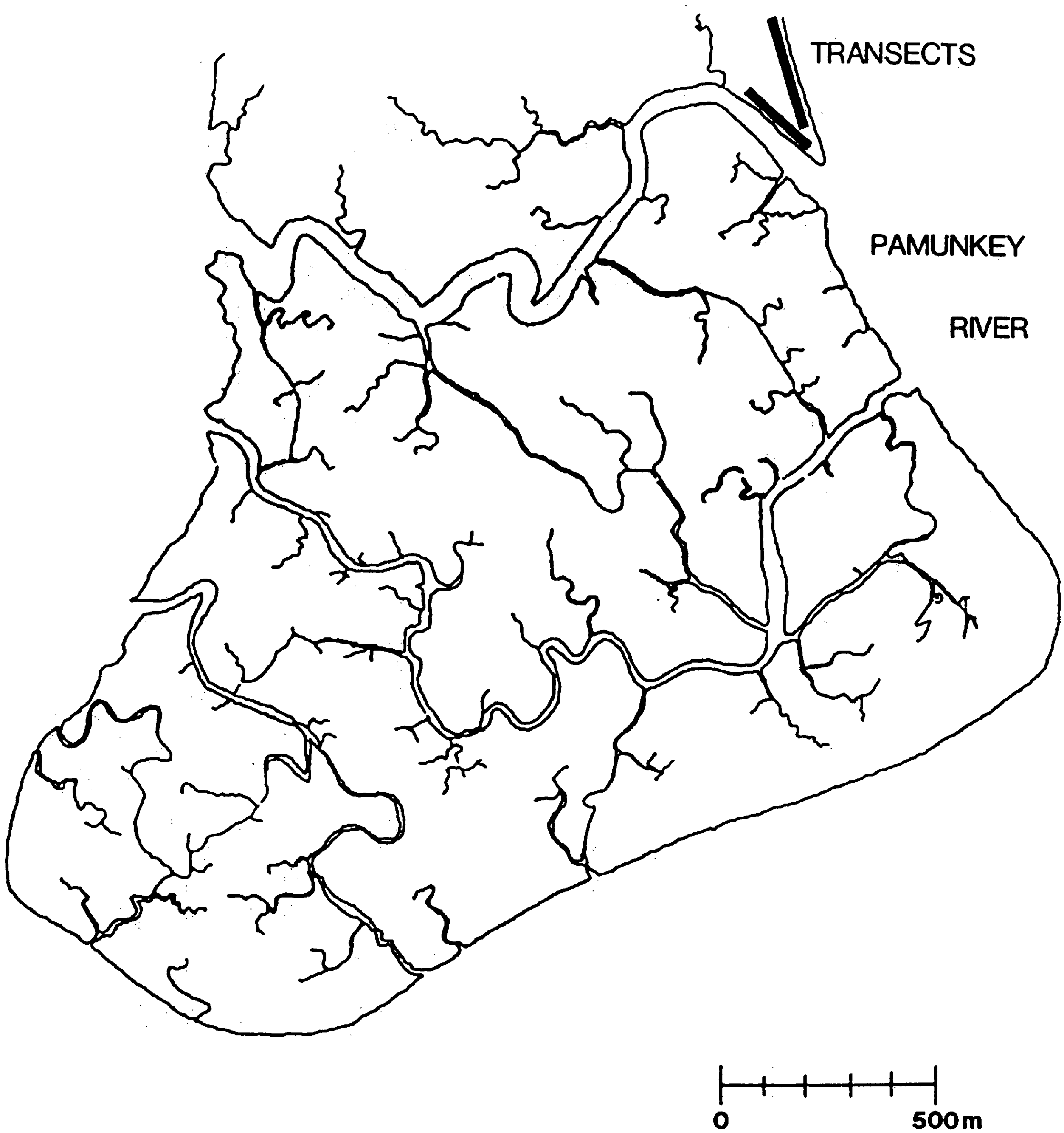

POTOMAC RIVER
RAPPAHANNOCK RIVER
MATTAPONI RIVER
PAMUNKEY RIVER
WEST POINT
YORK RIVER
JAMES RIVER
STUDY AREA
CHESAPEAKE BAY
EASTERN SHORE
ATLANTIC OCEAN
NAUTICAL MILES
0 5 10 15 20 25
0 10 20 30 40 50
KILOMETERS

Figure 2. Sampling locations in Sweet Hall Marsh, Virginia


TRANSECTS
PAMUNKEY
RIVER
0
500m

METHODS

To estimate production from the peak biomass and Smalley methods, harvesting was conducted from May to October 1986. Production from the mortality and Allen curve methods was estimated from data collected from tagged shoots in permanent plots from the end of April to the beginning of November 1986. Harvesting also was conducted in 1987 from May to October in the same transects. These data were used to compare annual production estimates from the 1986 and 1987 harvests to determine if there was variation in seasonal biomass accumulation and in the date of peak biomass. Following is a description of the field and analytical methods used to estimate production. Appendix 1 is an outline of the methods.

Peak Biomass

Ten 0.25 m^2 plots, five on the river and five on the creek, selected by random toss were harvested monthly from May through October 1986. Care was taken so previously harvested and trampled areas were not harvested. Corridors established landward of the plots were used to walk between plots. All standing live material was clipped at the sediment surface. All dead material standing or laying on the sediment was collected. Harvested material was placed in large plastic bags, returned to the lab and refrigerated 1 to 3 days until measured.

Shoots were thoroughly washed of mud, and sorted into the following groups; shoots with leaves, shoots without leaves, spathes (reproductive shoots), stipules, and decomposed material. Shoots with more than one leaf in a petiole were separated if readily pulled apart. Shoots with leaves were sorted into ten-centimeter size classes from 0.5 - 130 cm. Size class 1 included shoots from 0.5 - 9.9 cm, size class 2 included shoots from 10 - 19.9 cm and so on up to size class 13. Plants were dried at 60°C until a constant weight was achieved and then weighed to the nearest 0.01 g. Mean weights for each size class on each date were estimated by dividing the total weight for a size class by the number of shoots in that size class. The monthly data set with the largest mean standing crop was chosen as the estimate of the peak biomass.

Smalley's Method

The data used to estimate NAAP from Smalley's method were taken from the same harvest plots used to estimate the peak standing crop. Smalley's method attempts to account for mortality during the growing season by including the changes in harvested dead material. Production was estimated from the sum of the positive changes in live and dead biomass for each month. NAAP was calculated as follows:

1) If the net change between sampling periods was positive for both live and dead, then production was their sum.
2) If the change in live and dead were negative, production was assumed to be zero.

3) If the change in live was positive and the change in dead was negative, production was equal to the change in live.
4) If the change in live was negative and the change in dead positive, production was their sum, if the sum was greater than zero, and equal to zero if the sum was negative.

Mortality Method

The mortality estimate assumes a steady state system where annual production equals annual biomass lost to mortality. This is a good assumption for Peltandra because it completely dies back in the fall. To estimate NAAP from the summation of mortality a tagging study was conducted during the growing season of Peltandra, April to November 1986. To estimate mortality and monitor the life history of Peltandra, ten 0.25 m^2 quadrats were staked in March 1986. This was reduced to eight plots in June because the number of plots became unmanageable. Plots 1 and 6 were deleted. Four plots were located on the river and four on the creek in the same transects where harvesting was done. These plots were selected by tossing a staff from a boat and using the point where it landed as the center of the plot. At two week intervals during spring low tides, and when conditions permitted, the heights of all shoots and spathes were measured. Shoots with leaves were tagged and measured for total shoot height. Tagging was done by putting successive numbers on the upper surface of the leaves with permanent ink. On each successive tagging period all new shoots with leaves were measured and tagged and all previously tagged shoots were remeasured.

NAAP from mortality was estimated by summing the maximum mass reached by each shoot in the permanent plots which was recorded as biomass lost on the date of death. The date of death was assumed to be the date following the last measurement of the shoot. The mass of the shoot at death was estimated from the weight corresponding to the maximum height it reached during its life span. The heights of all shoots were divided into ten-centimeter size classes. The weight of each shoot was estimated from the size class weights from the harvests. Monthly size class weights were used because of variability within size classes between months. The weights from the harvest month nearest each tag date were used. Mortality for each size class for each sampling interval was the product of the number of shoots that died and the mass per shoot. All size classes then were summed for each date. Annual mortality for each plot was the sum of biomass lost over all sampling intervals. A mean of the eight plots was used to estimate NAAP from mortality. The peak biomass values of spathes and stipules were also added into the mortality estimate.

Allen Curve Method

To calculate production from the Allen curve tagged shoots were separated into cohorts. A cohort was defined as those shoots that were initially tagged on the same date. A graph of each cohort was made with the mean weight of an individual shoot in the cohort on the abscissa and the number of shoots in the cohort on the ordinate. Each point on the graph represented a date when that cohort was measured. The mean weight of a shoot in a cohort on each date was calculated by first sorting the shoots into size classes, applying the mean weight for each size class from the harvests, and calculating a mean weight for the cohort. Production for the cohort was proportional to the area beneath the curve. All cohorts in each plot were summed and the mean of the plots was used as the final Allen curve NAAP estimate.

Population Parameters

Populaton parameters measured or calculated included daily production and mortality rates, shoot density, life span, recruitment, and turnover. Production rates were calculated for each harvest interval by dividing the biomass changes between sampling intervals by the number of days in the interval. Life span of shoots was estimated from the date a shoot first was tagged to the date following the last measurement. Recruitment was estimated from the number of shoots newly tagged on each date.

Daily mortality rates were calculated by dividing the mean biomass from mortality for each tagging interval by the number of days in the interval. Percent mortality for each time interval was an estimate of dead material produced from an amount of live material present. It was calculated for each interval by dividing the daily mortality rates by the live biomass present during the same time interval. The live biomass estimates were from the harvested live material and live material estimated from the Allen curve which resulted in two estimates of percent mortality. The mean biomass from the two Allen curve dates that matched the mortality interval were used to get the best estimate of live biomass for the interval.

Annual turnover was calculated by three methods. Shew's "experimental turnover rate" was calculated by dividing the number of days in the growing season by the mean life span of a shoot. The growing season was estimated as the time this study covered, April 26, to November 4, 1986. The other two methods were ratios; NAAP (from mortality) to peak biomass and NAAP to mean biomass.

RESULTS

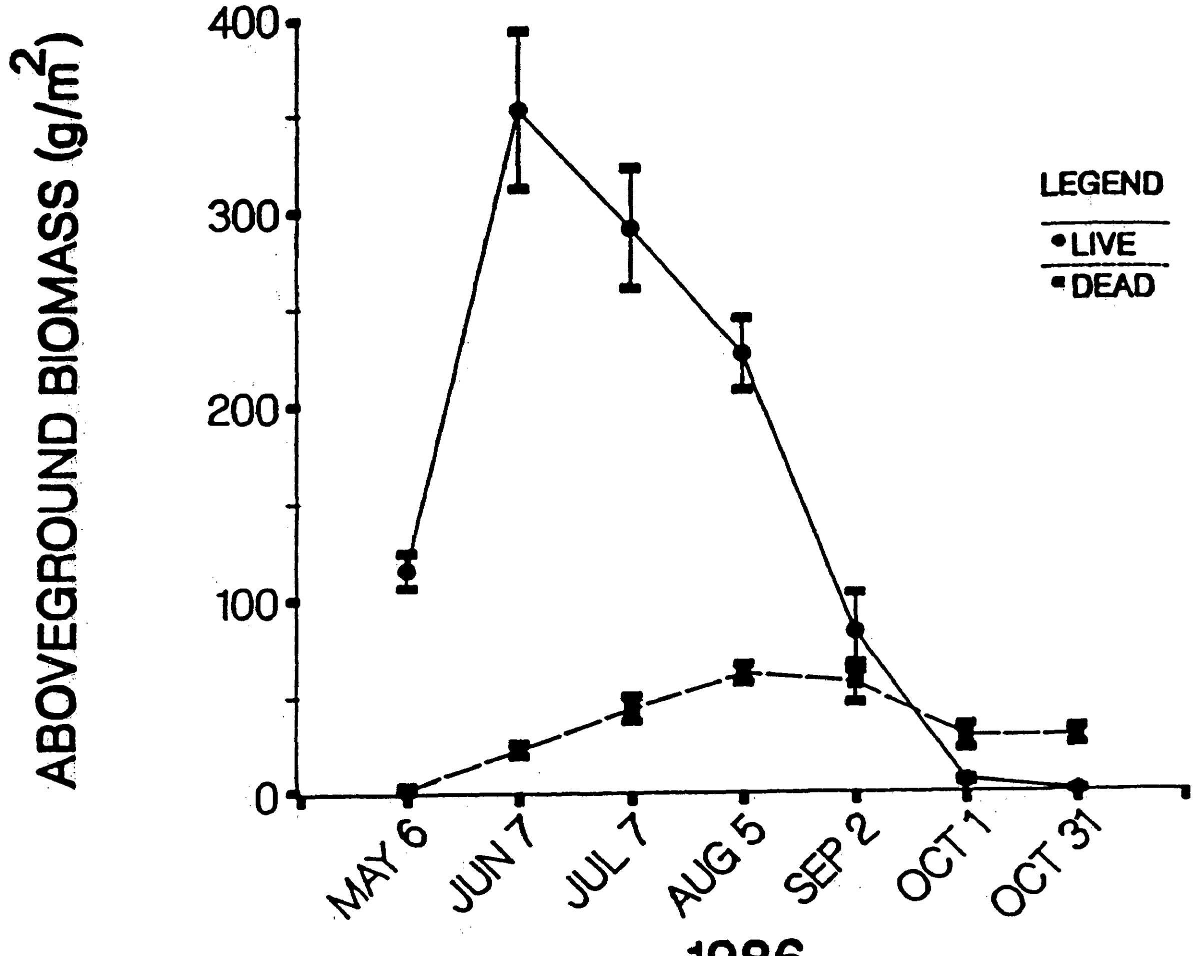
Peak Biomass Method

From November 1985 to February 1986 the study area was without vegetation, as aboveground shoots of _Peltandra_ completely die back in winter. Observations in March 1986 indicated the presence of new growth but no leaves had yet formed. On April 26, the first leaves were observed; they were very small and only a few were present. However, by the first harvest on May 6, 1986, 115.52 g/m^2 were present (All biomass values are in dry weights, dwt). Peak biomass was reached on June 7 with 352.64 g/m^2 (Figure 3). The first harvest in 1987 was on May 15 with a mean biomass of 220.20 g/m^2. Peak biomass was reached on July 16 with 437.48 g/m^2 (Figure 4).

Smalley's Method

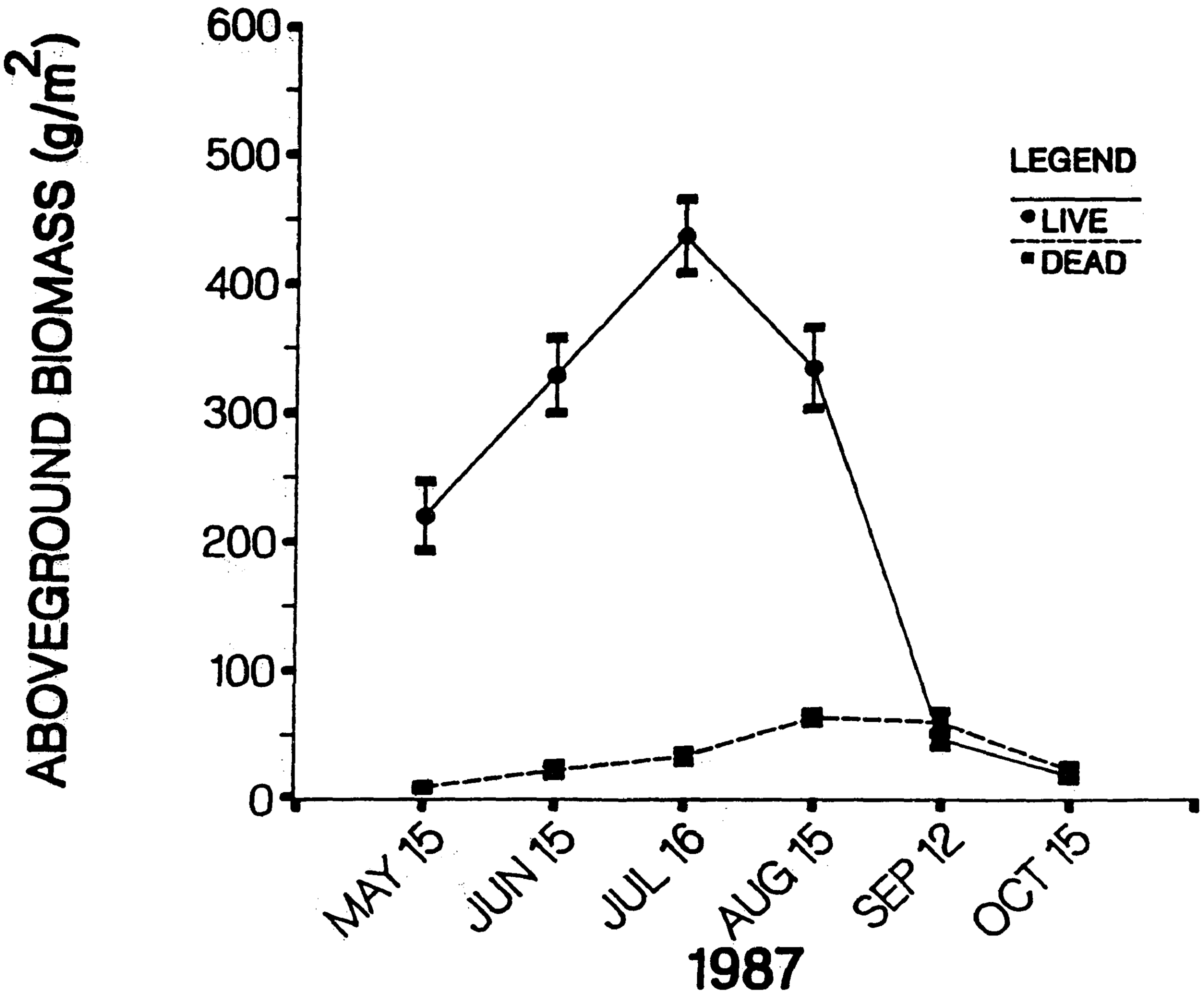
In 1986, the Smalley method accounted for a minimal amount of mortality between sampling intervals resulting in a net production estimate of 375.44 g/m^2/year, which was 6.0% greater than the peak biomass estimate. Dead biomass collected included standing dead, fallen shoots, and stipules. Most of the fallen shoots were still attached to

Figure 3. Aboveground live and dead biomass (g dwt/m^2) in 1986, n=10. Ranges represent $\pm$ 1 standard error.



ABOVEGROUND BIOMASS (g/m2)
400
300
200
100
0
LEGEND
• LIVE
▪ DEAD
MAY 6
JUN 7
JUL 7
AUG 5
SEP 2
OCT 1
OCT 31
1986

Figure 4. Aboveground live and dead biomass (g dwt/m^2) in 1987, n=8 except on May 15 n=7. Ranges represent $\pm$ 1 standard error.

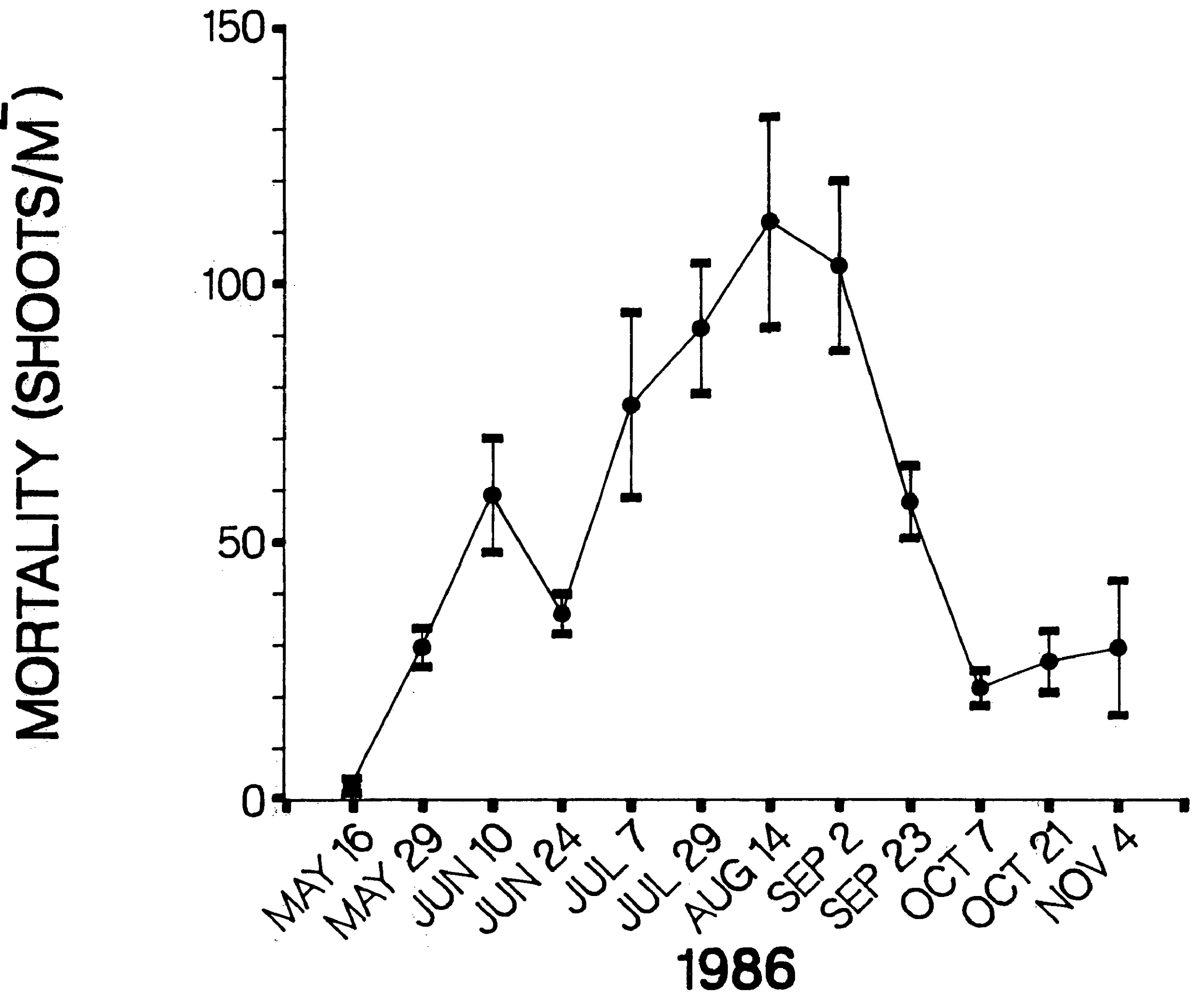

ABOVEGROUND BIOMASS (g/m2)
600
500
400
300
200
100
0
LEGEND
LIVE
DEAD
MAY 15
JUN 15
JUL 16
AUG 15
SEP 12
OCT 15
1987

the plant by vascular tissue. Dead material peaked in August at 61.6 g/m^2 (Figure 3) and 63.76 g/m^2 (Figure 4) in 1986 and 1987, respectively. After the peak, negative changes in live biomass were greater than the positive changes in dead biomass, therefore net production was assumed to be zero.

Mortality Method

The mortality production estimate from shoots was 714.20 g/m^2/year, calculated from a mean of all plots. Because spathes and stipules were not tagged their peak biomass, 75.24 g/m^2 in June, was added to this number resulting in a NAAP of 789.44 g/m^2/year. NAAP estimated by the mortality method was 2.24 times greater than the peak biomass method and 2.10 times greater than the Smalley method. The greatest number of shoots that died in the tagged plots was counted on August 14 and equaled 112.0 shoots/m^2 (Figure 5). To determine the biomass of the dead shoots, mean mass for each size class was calculated from each harvest. Monthly mean weights were used because an ANOVA of the shoot size-class average weights indicated a significant seasonal variation ($P < 0.05$) (Table 1). Size classes 8 - 13 were only present from June 7 to September 2 (Table 1). The plot with the largest estimated biomass from mortality was plot 8 with 1535.16 g/m^2 (Table 2). The interval with the largest biomass lost to mortality was July 29 to August 14 with 176.04 g/m^2 (Table 3).

Figure 5. Mean number of shoots (shoots/m^2) that died on each tagging date, n=8. Ranges represent $\pm$ 1 standard error (1986).



MORTALITY (SHOOTS/M^2)
150
100
50
0
MAY 16
MAY 29
JUN 10
JUN 24
JUL 7
JUL 29
AUG 14
SEP 2
SEP 23
OCT 7
OCT 21
NOV 4
1986

Table 1. Monthly harvest mean weights (g) for each size class from 1986 harvest.

Date	Size Class												
	1	2	3	4	5	6	7	8	9	10	11	12	13
May 6	0.06	0.12	0.18	0.39	0.66	1.05	1.37	-	-	-	-	-	-
Jun 7	-	-	0.26	0.23	0.31	0.55	0.67	1.00	1.79	2.42	3.11	3.24	3.66
Jul 7	-	-	0.09	0.16	0.35	0.47	0.66	0.93	1.33	2.35	2.38	3.30	-
Aug 5	-	-	0.09	0.17	0.24	0.46	0.61	1.01	1.50	1.96	2.69	2.89	-
Sep 2	-	0.02	0.12	0.26	0.38	0.68	1.02	1.25	1.49	1.65	-	-	-
Oct 1	-	0.05	0.11	0.19	0.34	0.51	0.51	-	-	-	-	-	-
Oct 31	0.02	0.04	0.10	0.30	-	-	-	-	-	-	-	-	-

Table 2. Biomass from tagged shoot mortality summed over the 1986 growing season for each plot (g dwt/m^2).

Plot	(g dwt/m^2)
2	545.96
3	649.72
4	194.40
5	38.92
7	735.44
8	1535.16
9	636.72
10	1377.28

Table 3. Mean biomass lost to mortality (g dwt/m^2), daily rates of mortality (g dwt/m^2/day), and percent mortality per day (%/day) for each tagging interval. Live aboveground biomass from the Allen curve (g dwt/m^2). Range represents ± 1 standard error, n=8 except where (*) n=7 (1986).

Tagging Interval End Date	Mortality (g/m^2)	Days in Interval	Mortality Rates (g/m^2/day)	Allen Biomass (g/m^2)	Percent Mortality (%/day)
5/16	1.72 ± 1.71	21	0.08	108.24	0.07
5/29	25.80 ± 6.93	14	1.84	277.24	0.66
6/10	57.00 ± 23.93	13	4.38	336.60	1.30
6/24*	136.08 ± 11.48	15	2.41	389.16	0.62
7/7	103.28 ± 54.08	14	7.38	393.60	1.87
7/29	123.52 ± 33.70	23	5.37	311.92	1.72
8/14	176.04 ± 72.21	17	10.36	229.16	4.52
9/2*	47.36 ± 59.49	20	7.37	121.88	6.04
9/23*	59.92 ± 16.31	22	2.72	46.44	5.86
10/7*	14.11 ± 6.09	15	0.94	14.40	6.53
10/21*	9.18 ± 5.37	15	0.61	9.32	10.76
11/4	8.54 ± 7.55	15	0.57	4.92	11.57

Allen Curve Method

The Allen curve method yielded an annual aboveground production of 823.10 $g/m^2/year$ which is 4.0% greater than the estimate from the mortality method. The May 16 cohort had the largest estimated biomass, 228.76 g/m^2 from the Allen curve (Figure 6). An example of the Allen curve is in Figure 7. Plot 8 had the largest biomass, 1589.64 g/m^2 and plot 5 the smallest with 42.8 g/m^2 as estimated by the Allen curve (Table 4).

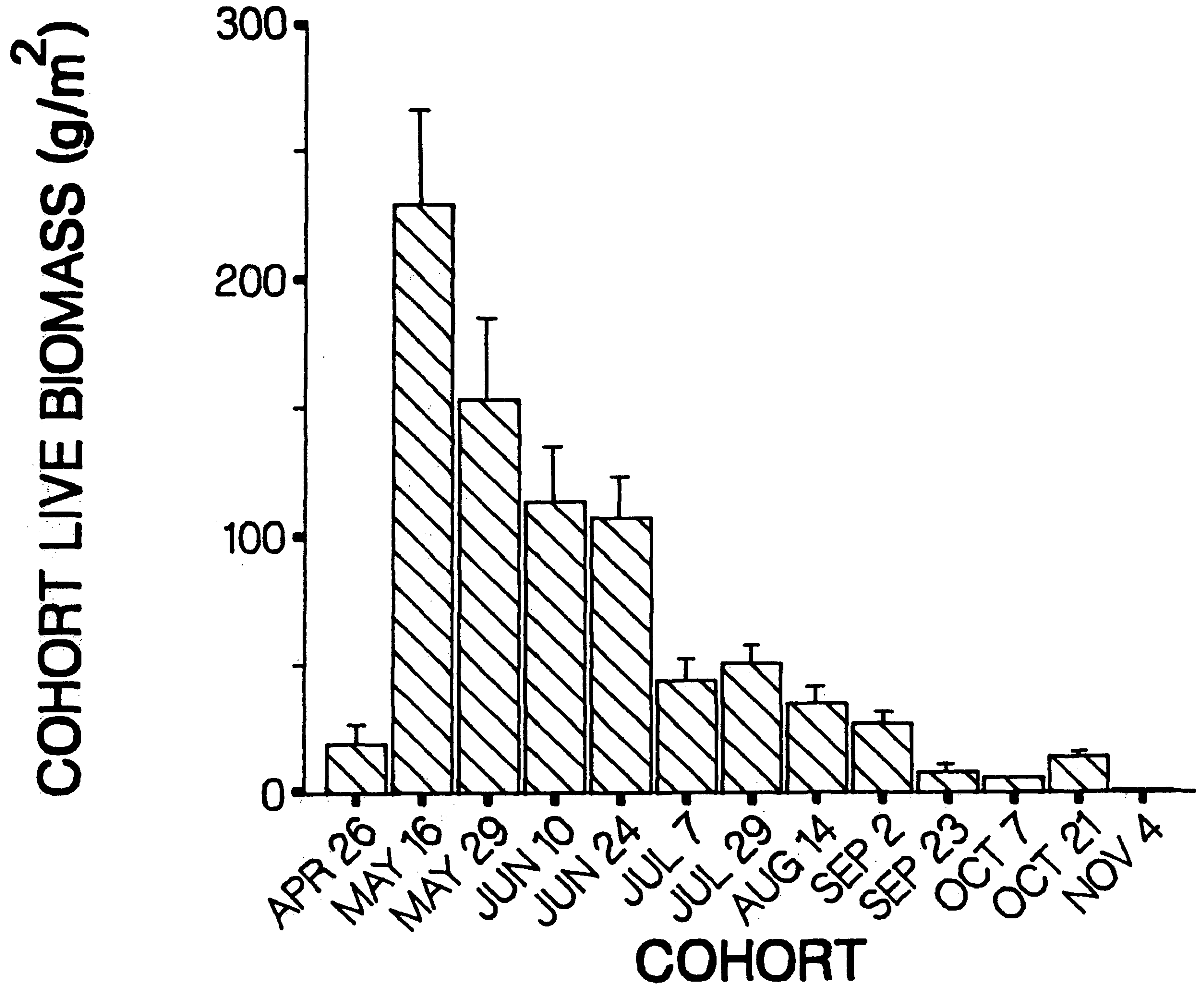
The mortality and Allen curve estimates were not significantly different from each other ($P < 0.05$) and they were both more than two times greater than the peak biomass and Smalley estimates (Table 5).

Population Parameters

Production rates up to peak were 7.41 $g/m^2/day$ for 1986 and 3.40 $g/m^2/day$ in 1987. Production rates declined after the June peak in 1986 and 1987 (Tables 6,7).

Mortality rates per day ranged from 0.08 g/m^2 from April 26 to May 16 to the maximum rate, 10.36 g/m^2, between July 29, and August 14 (Table 3). Percent mortalities ranged from 0.07% per day between April 26 and May 16, to 11.57% per day from October 21 to November 4 (Table 3). Percent mortality per day also was calculated on the basis of harvested live biomass; the range was 0.07% for May to 30.21% for late October (Table 8). The high value for late October was a result of

Figure 6. Mean live biomass (g dwt/m^2) for each cohort calculated from the Allen curve, n=8, except when plot 10 was not sampled (June 10, July 7, August 14, September 23, and October 7). Ranges represent $\pm$ 1 standard error (1986).



COHORT LIVE BIOMASS (g/m²)
300
200
100
0
APR 26
MAY 16
MAY 29
JUN 10
JUN 24
JUL 7
JUL 29
AUG 14
SEP 2
SEP 23
OCT 7
OCT 21
NOV 4
COHORT

Figure 7. Allen curve of the June 10 cohort in plot 3.

ALLEN CURVE FOR JUNE 10 COHORT
PLOT 3

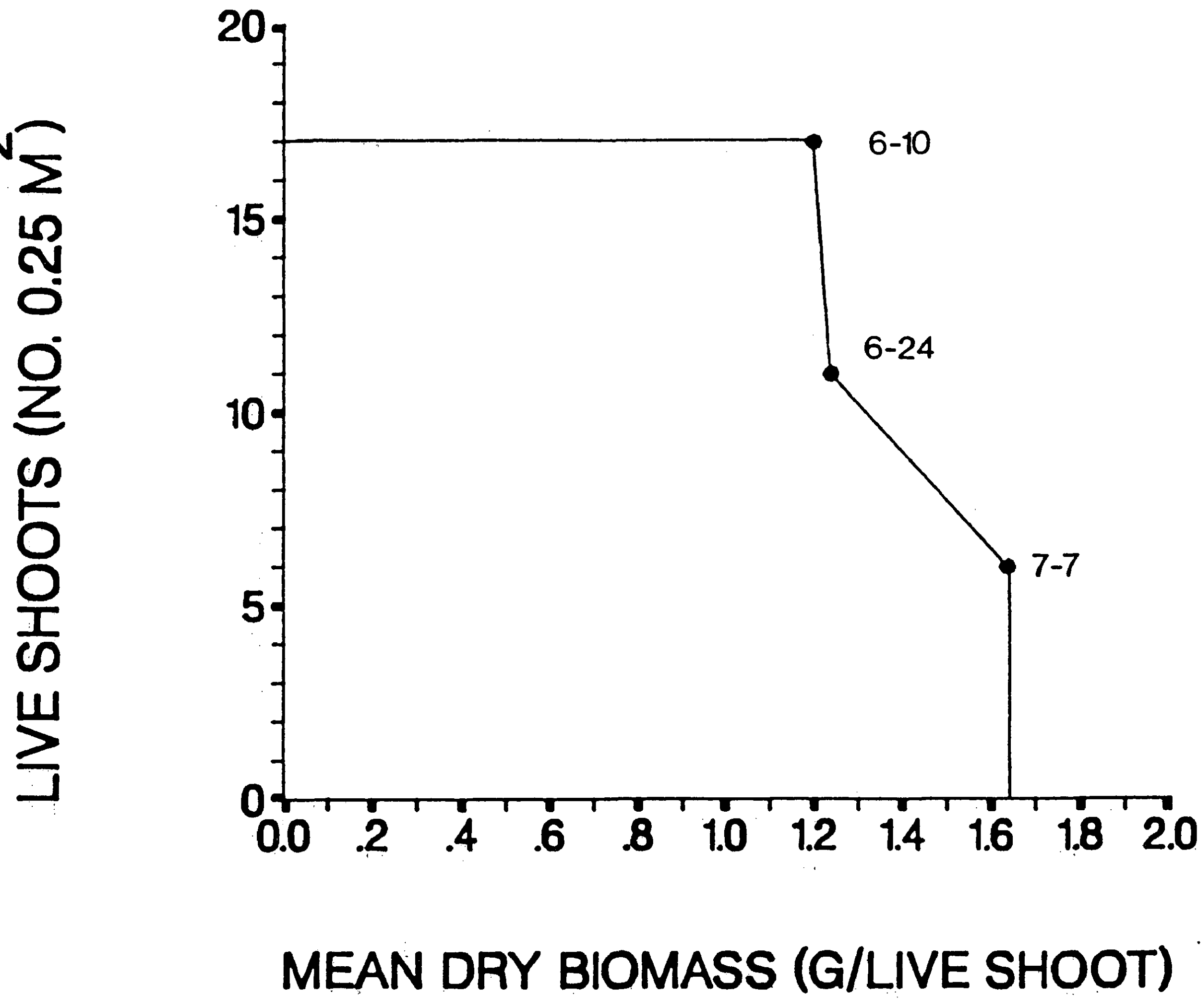


Table 4. Live biomass from the Allen curve summed over all tagging periods for each plot (g dwt/m^2) (1986).

Plot	Live Biomass (g dwt/m^2)
2	581.04
3	756.16
4	224.04
5	42.80
7	775.60
8	1589.64
9	647.04
10	1366.52

Table 5. Net annual aboveground primary production (g dwt/m^2/yr) for *Peltandra virginica* obtained from four methods (1986).

METHOD	SAMPLING TYPE	BIOMASS (g dwt/m^2/yr)
PEAK BIOMASS	harvest	352.64
SMALLEY	harvest	375.44
MORTALITY	tagging	789.44
ALLEN CURVE	tagging	823.10

Table 6. Aboveground live biomass (g dwt/m^2) and production rates (g dwt/m^2/day) in 1986 for Peltandra. Ranges represent ± 1 standard error; n=10.

DATE	LIVE BIOMASS (g dwt/m^2)	PRODUCTION RATES (g dwt/m^2/day)
May 6	115.52 ± 17.70	
June 7	352.64 ± 81.24	7.41
July 7	291.20 ± 61.72	-2.05
August 5	226.20 ± 36.92	-2.24
September 2	82.84 ± 39.88	-5.12
October 1	6.00 ± 1.84	-2.65
October 31	0.96 ± 0.48	-0.17

Table 7. Aboveground live biomass (g dwt/m^2) and production rates (g dwt/m^2/day) in 1987 for <u>Peltandra</u>. Ranges represent ± 1 standard error; n=8 except on May 15 n=7.

DATE	LIVE BIOMASS (g dwt/m^2)	PRODUCTION RATES (g/m^2/day)
May 15	220.20 ± 53.72	
June 15	329.28 ± 58.28	3.41
July 16	437.48 ± 56.96	3.38
August 15	335.16 ± 62.92	-3.30
September 12	47.08 ± 12.00	-9.92
October 15	18.24 ± 5.52	-0.87

Table 8. Mortality rates per day (g dwt/m^2/day), harvested live biomass (g dwt/m^2), and percent mortalities per day. The mean mortality rate per day was used when two tag dates were used for one harvest (1986).

Tag Date	Mortality Rates (g/m^2/day)	Harvest Date	Live Biomass (g/m^2)	Percent Mortality per day (%/day)
5/16	0.08	5/6	115.52	0.07
5/29 6/10	1.84 4.38	6/7	352.64	0.87
6/24 7/7	2.41 7.38	7/7	291.20	1.68
7/29 8/14	5.37 10.36	8/5	226.20	3.48
9/2	7.37	9/2	82.84	8.90
9/23 10/7	2.72 0.94	10/1	6.00	10.42
10/21 11/4	0.61 0.57	10/31	0.96	30.21

the proportionately high mortality rate as compared to the live biomass in the plots.

Plant density in the tagged plots was 18% greater than in the harvest plots. The annual mean in the tagged plots was 128.40 shoots/m^2, harvest plots had a mean of 108.44 shoots/m^2. The greatest density in the tagged plots was on June 24 with 276 shoots/m^2 (Figure 8). The 1986 harvest plots had a maximum density in June with 220 shoots/m^2 (Figure 9).

The average life span of all tagged shoots was 53 days, with a range of 40 - 68 days between plots. The range for individual shoots was 14 - 125 days. The May 29 cohort had the longest life span with 67 days (Figure 10).

Shoots were recruited on all sampling dates; with the peak on May 16 with 164 shoots/m^2 (Figure 11). There was a large recruitment between April 26, when only 13 shoots/m^2 shoots were present, and the May peak. The total number of shoots tagged in the eight 0.25 m^2 quadrats was 1202. Plot 10 had the largest recruitment with 283 shoots/0.25 m^2 and plot 5 had the least with only 9 shoots/0.25 m^2 (Table 9).

Turnover rates were calculated by three methods. A turnover rate of 3.6 was calculated by dividing the number of days in the growing season, 191 days, by the mean life span. The growing season was estimated as the number of days between the first and last samples in this study. Turnover calculated by the ratio of NAAP to peak biomass was 2.24; and the ratio of NAAP to the mean biomass, 153.62 g/m^2, was 6.83.

Figure 8. Mean density (shoots/m^2) for each tagging period, n=8 except when plot 10 was not sampled (June 10, July 7, August 14, September 23, and October 7). Ranges represent $\pm$ 1 standard error (1986).

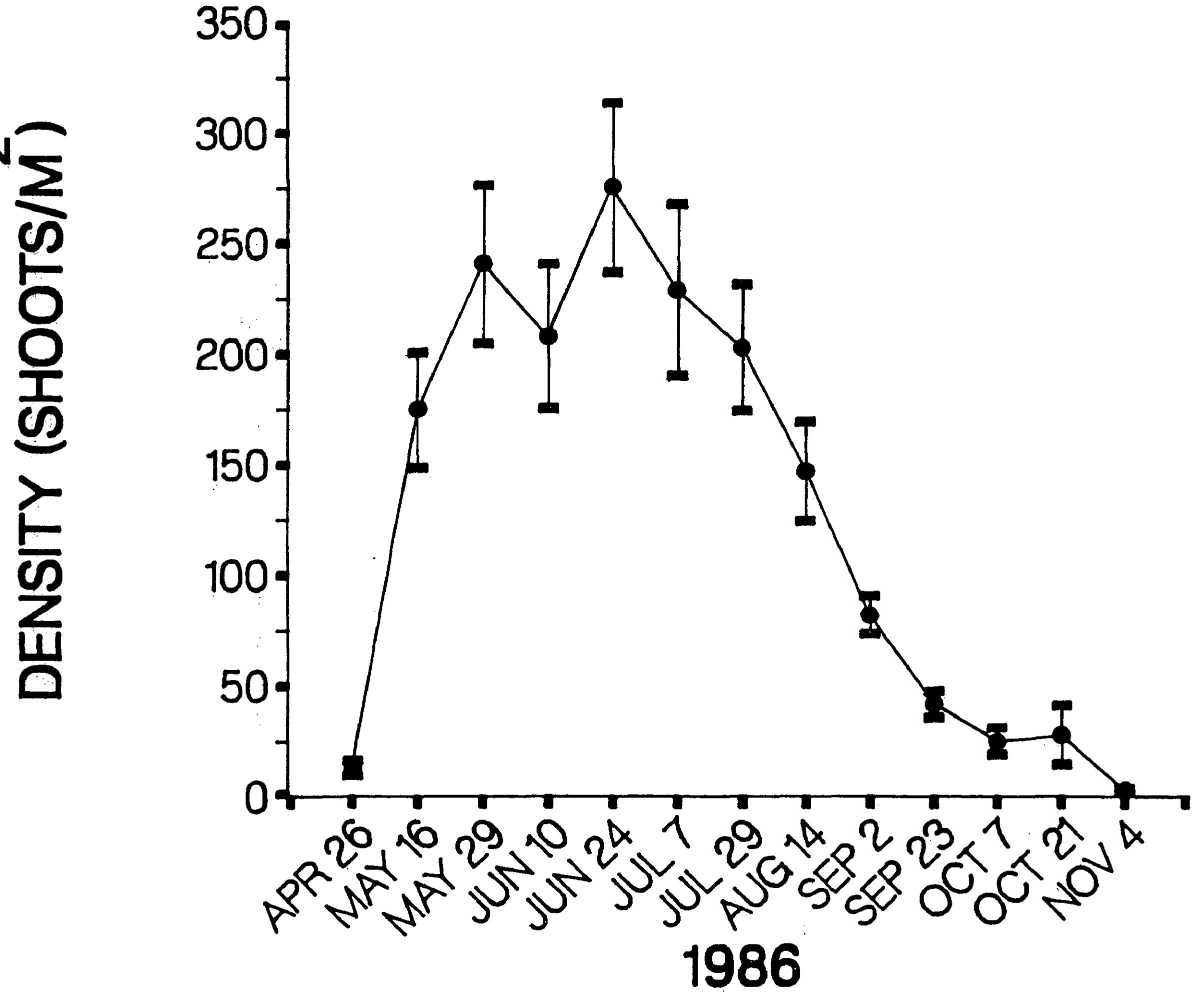
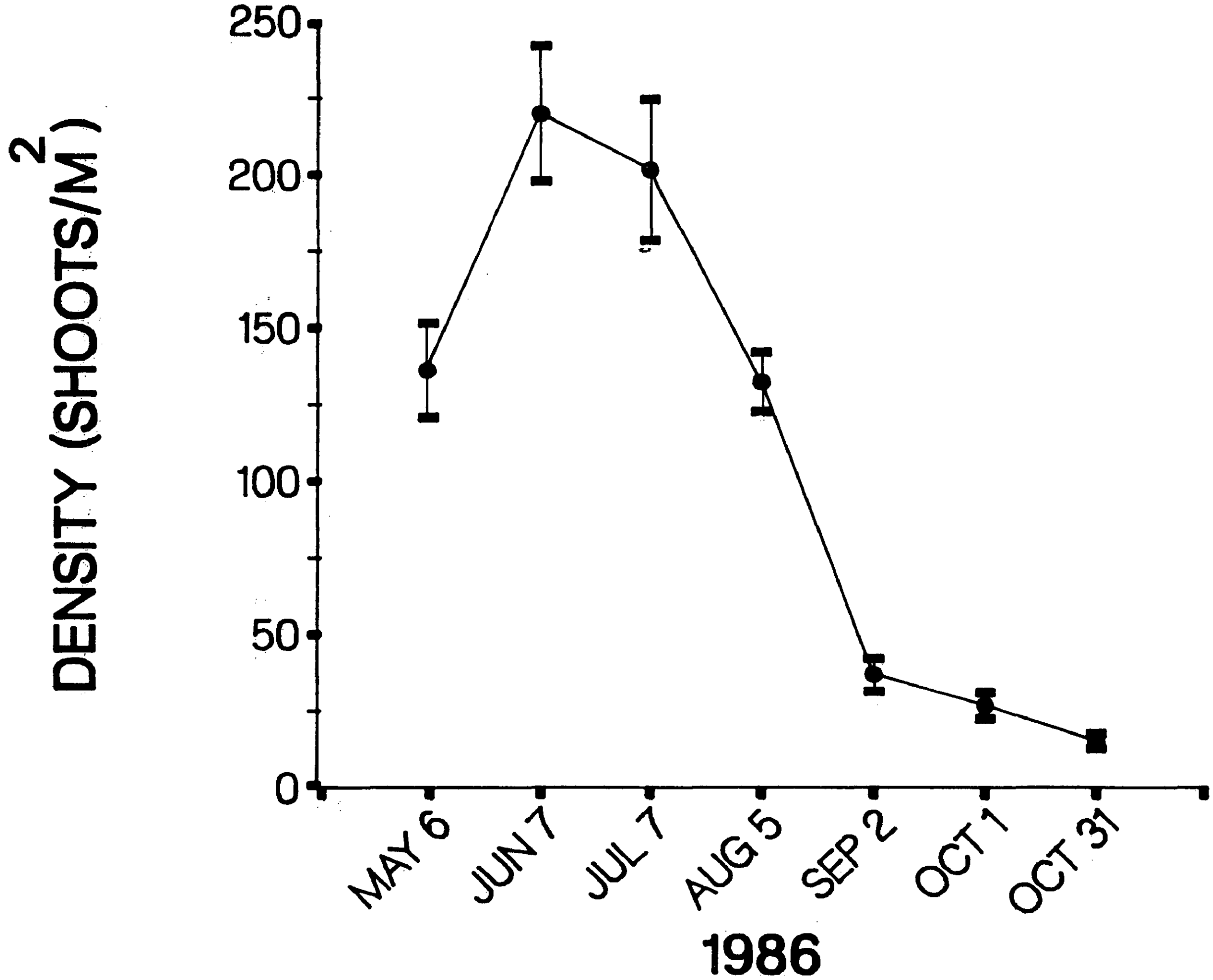

DENSITY (SHOOTS/M^2)
350
300
250
200
150
100
50
0
APR 26
MAY 16
MAY 29
JUN 10
JUN 24
JUL 7
JUL 29
AUG 14
SEP 2
SEP 23
OCT 7
OCT 21
NOV 4
1986

Figure 9. Mean density (shoots/m^2) of live shoots in 1986 harvest plots. Ranges represent $\pm$ 1 standard error.



DENSITY (SHOOTS/M^2)
250
200
150
100
50
0
MAY 6
JUN 7
JUL 7
AUG 5
SEP 2
OCT 1
OCT 31
1986

Figure 10. Mean life span (days) of each cohort, n=8 except when plot 10 was not sampled (June 10, July 7, August 14, September 23, and October 7) (1986).

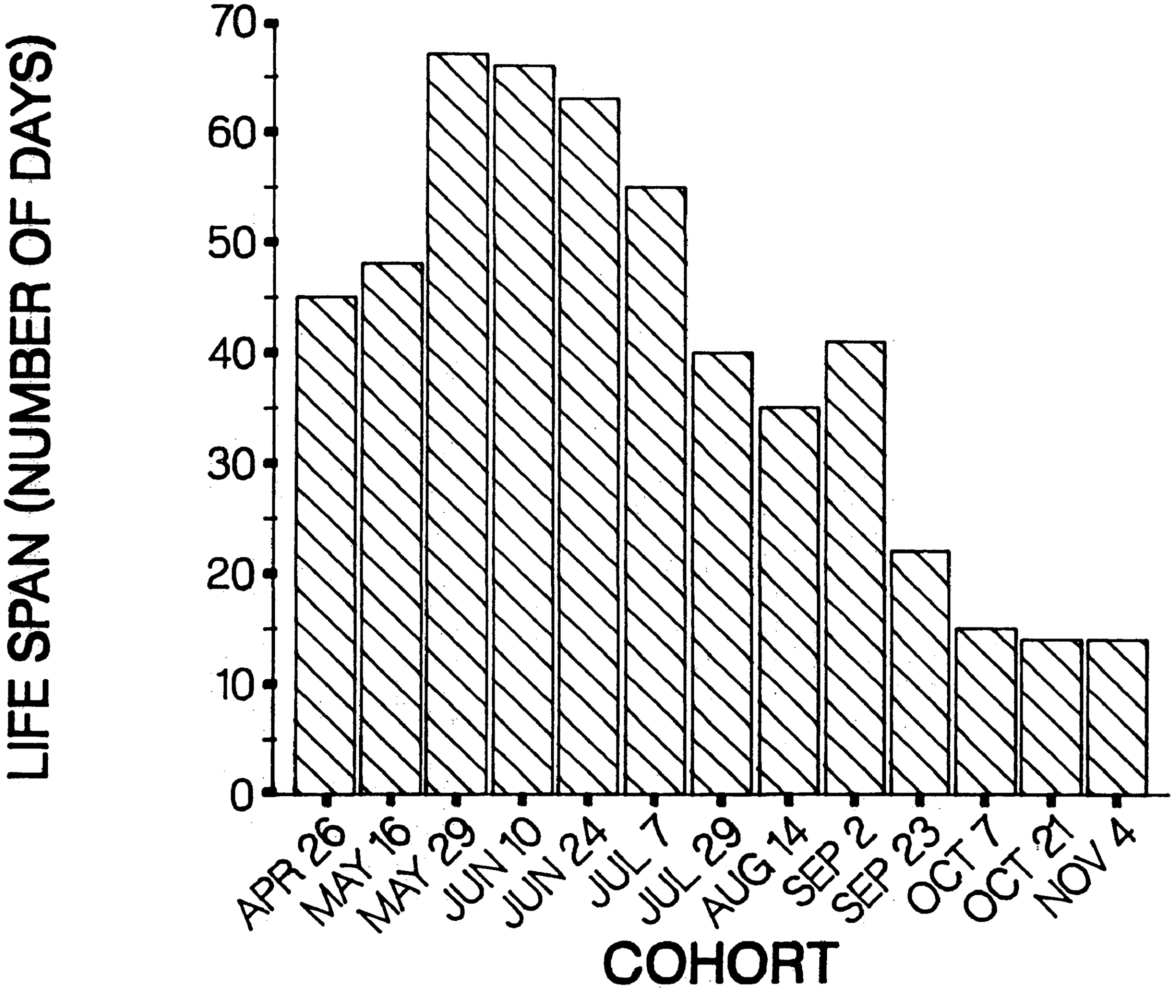

LIFE SPAN (NUMBER OF DAYS)
70
60
50
40
30
20
10
0
APR 26
MAY 16
MAY 29
JUN 10
JUN 24
JUL 7
JUL 29
AUG 14
SEP 2
SEP 23
OCT 7
OCT 21
NOV 4
COHORT

Figure 11. Mean recruitment (shoots/m^2) of shoots on each tagging period, n=8 except when plot 10 was not sampled (June 10, July 7, August 14, September 23, and October 7). Ranges represent $\pm$ 1 standard error (1986).

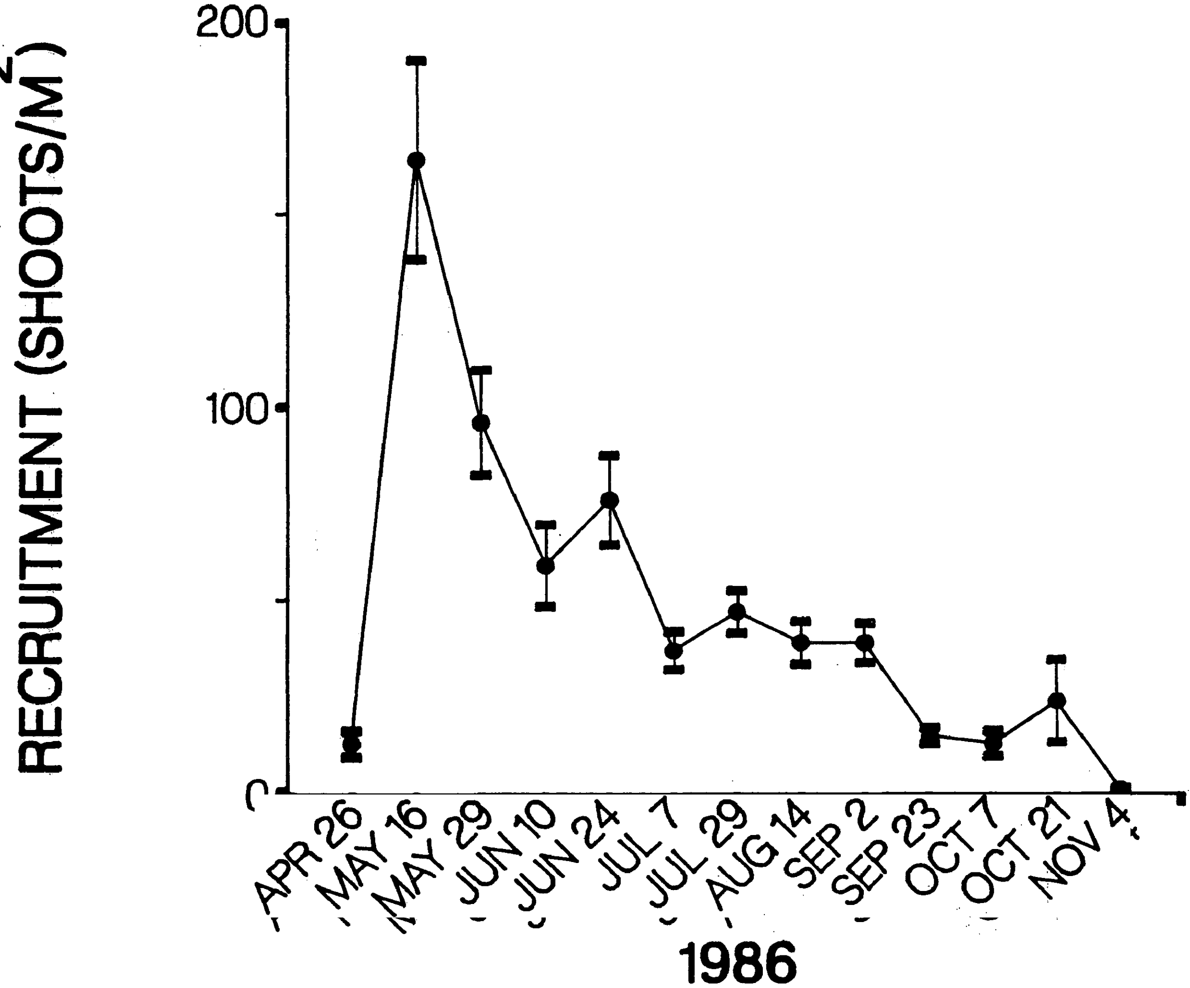

RECRUITMENT (SHOOTS/M2)
200
100
0
APR 26
MAY 16
MAY 29
JUN 10
JUN 24
JUL 7
JUL 29
AUG 14
SEP 2
SEP 23
OCT 7
OCT 21
NOV 4
1986

Table 9. Number of shoots recruited in each plot (shoots/0.25 m^2) (1986).

Plot	Shoots/0.25 m^2
2	160
3	165
4	50
5	9
7	152
8	280
9	103
10	283

DISCUSSION

Peak Biomass

The peak biomass method is a widely used method because of its simplicity, albeit, it is well documented that it results in significant underestimates of NAAP (Mason and Bryant, 1975; Whigham et al., 1978). The peak biomass reported in this study was early in the growing season and represented only a portion of total net aerial production. Other studies that reported peak biomass estimates for *Peltandra* also found an early spring peak. Other peak biomass estimates generally were greater than those reported in this study. Walker (1981) and Booth (1989) sampled in monospecific stands of *Peltandra*. Booth reported a peak standing crop of 969 g/m^2 in July for a creek bank stand in Sweet Hall Marsh. The *Peltandra* plants in Booth's plots generally were larger and more dense than the plots in this study, which may account for the difference in the biomass values. His samples also were biased to include large amounts of biomass in each harvest for nutrient analysis. Walker (1981) harvested every two weeks in two areas of *Peltandra* in New Jersey, one area with poorly drained soils and a second area with a better drained substrate, the peak aerial live biomasses were 452 g/m^2 on June 10 and 637 g/m^2 on July 2, respectively.

Pickett (1984) and Doumlele (1981) reported peak standing crops for Peltandra in heterogeneous communities. In a mixed community, where Peltandra only accounted for 5.2% of the production, Pickett harvested 40.5 g/m^2 on May 1 and the peak biomass, 84.0 g/m^2, on June 2. Doumlele (1981) harvested Peltandra in a mixed community in Sweet Hall Marsh and reported an initial standing crop of 297.83 g/m^2 in May and a peak biomass of 423.40 g/m^2 in June. He had a higher initial standing crop, but the peak was not much larger than that reported in the present study. Peltandra, however, only accounted for 55% of the community production in his study. Doumlele's initial and peak standing crops may have been proportionately larger than the standing crops reported in the present study because of the geomorphological differences between the two study sites. His transects extended from the streamside community landward, through areas of higher elevations with better drainage than where the present study was conducted. Walker (1981) reported higher production estimates for Peltandra in better drained soils. I observed that the Peltandra in the mixed community at higher elevations produced leaves earlier than in the monospecific intertidal stands where this study was conducted.

Smalley's Method

The Smalley estimate for NAAP was only slightly greater than the peak biomass estimate. The difference may be attributed to the additional biomass included in the NAAP from the harvested dead. The purpose of including the seasonal changes in the harvested dead was to account for mortality. However, this method did not account for an appreciable amount of mortality because of its dependence on the collection of dead material, which is very difficult with Peltandra because of its fast decomposition rate (Odum and Heywood, 1978). The one meter tidal exchange in Sweet Hall also removes a portion of the dead material before it can be collected. Most studies reported that the Smalley method underestimates production because it does not account for all mortality and decomposition between sampling periods, or for production after peak (Linthurst and Reimold, 1978; Shew et al., 1981; and Giroux and Bedard, 1988). Hopkinson et al. (1980) found Smalley's method resulted in a slightly greater NAAP estimate than peak biomass but recommends not using this method for species with constant growth, seasonal mortality, and disappearance of dead material.

Mortality Method

Studies in tidal fresh wetlands that have compared production estimates from harvest methods with mortality estimates from tagged shoots also reported greater estimates when mortality was included. Booth's (1989) production estimate for Peltandra was 1634.44 g/m^2/year, which was calculated using the mortality rates derived in the present study and then corrected for the variations between the reported harvest values for 1987 in the two studies. Pickett (1984) used mortality rates to augment her production estimate from harvests, resulting in a production estimate 2.87 times peak biomass. This was similar to the difference between the mortality and peak biomass production estimates reported in this study: mortality was 2.24 times greater than the peak biomass. Pickett also reported that leaf production after peak biomass accounted for an additional 35% of NAAP. Gosselink et al. (1977) estimated production for Sagittaria falcata, a tidal freshwater plant morphologically similar to Peltandra, and reported a production estimate from the summation of mortality to be 1.7 times greater than the peak biomass estimate. Hopkinson et al. (1980) reported a production estimate including mortality that was 3.56 times greater than the peak biomass estimate for Sagittaria falcata.

In other ecosystems production studies that included mortality resulted in production estimates that were greater than harvest production estimates. Studies in salt marshes have shown that when mortality is included production estimates are 8 to 75% greater than both the peak biomass and the sum of changes in biomass (Gallagher et al., 1980; Reidenbaugh, 1983; Houghton, 1985). Gosselink et al. (1977) compared five methods of estimating NAAP of seven marsh plants in Louisiana estuarine marshes and reported that the Smalley method was 27% lower than their mortality method. Hopkinson et al. (1980) reported production estimates for salt marsh plants including mortality that ranged from 1.4 to 3.06 times greater than peak biomass estimates. In sedge meadows, Bernard and MacDonald (1974) and Bernard and Hankinson (1979) found that when mortality was incorporated into production estimates they were 1.8 to 2.0 times greater than production estimated from the change between the maximum and minimum biomass.

Allen Curve Method

The Allen curve results were very similar to those of the mortality method: this was expected because they both accounted for density and mass changes in the permanent plots. Though different masses for each shoot were used in each method. In the mortality calculations the number of shoots in each size class was multiplied by the maximum size class weight they reached. In the Allen curve the number of shoots in a cohort was multiplied by the mean weight of the cohort, assuming that all shoots in a cohort have the same mean weight. The cohorts in the present study were comprised of many size classes and weights, negating this assumption. Dickerman et al. (1986) found similar results with their summed shoot maximum method and the Allen curve. Dickerman et al. point out that the Allen curve is a good method to use for production estimates, and also has the advantage of including population parameters such as turnover, early plant mortality, and longevity. These population parameters greatly influence NAAP, but typically are not measured in production studies (Bernard and MacDonald, 1974; Bernard and Hankinson, 1979; Dickerman et al., 1986).

As with all techniques requiring direct measurements of individuals, field and analysis time for the Allen curve is very intensive and expensive. The Allen curve can be constructed more quickly than the method used in this study by simply measuring density and deriving a mean weight of only a few shoots in each cohort, instead of all shoots as was done in this study. This would be especially useful in plant populations where the mean weight of a cohort is not as variable as with Peltandra. Dickerman et al. (1986) suggested that the Allen curve can be used to identify quickly the dynamics of the population. For example, to maximize sampling efficiency more sampling effort can be devoted when density or mean shoot biomass show great fluctuations than in periods of minimal change. Mathews and Westlake (1969) also suggest that the Allen curve can be used to observe seasonal changes in negative production and mortality. Another advantage of the Allen curve is its relative insensitivity to sampling frequency (Dickerman et al., 1986).

In the present study, the cohort with the maximum biomass estimated by the Allen curve was the May cohort. This may be due to both the high shoot weights in May and to the large number of recruits in this cohort. For most size classes, the highest shoot weight was in May. This seasonal variation in shoot weights may be attributed to the life history of Peltandra. The shoots in May are heavy because enclosed in their petioles are developing shoots that emerge later in the season forming new shoots.

Population Parameters

Trends in live and dead biomass generally showed an early fast growth, high mortality, and recruitment that continued throughout the year. Walker (1981) suggested that the fast early production in Peltandra is due to rhizome translocation of nitrogen and phosphorus to the new aerial shoots. He found that in the spring, 45% of these aerial nutrients were from rhizome stores. Doumlele (1981), Walker (1981) and

Pickett (1984) also observed an early fast growth for *Peltandra*. Seasonal standing crops and production rates for *Peltandra* did vary among these studies, due in part to the clumped nature of the plants and the morphological variations in the leaves. Daily production rates for *Peltandra* are high in the early spring up to the peak, and thereafter decline. The daily production rates in this study up to peak were 7.41 g/m^2 and 3.41 g/m^2 in 1986 and 1987, respectively. Walker (1981) reported daily production rates to the peak were 10.49 g/m^2 in a poorly drained site, and 9.74 g/m^2 in a better drained site. Walker also cited Whigham and Simpson (1975), who reported daily production rates for *Peltandra* ranging from 6.0 to 13.4 g/m^2 on the Delaware River from April 25 to May 30, and 2.6 to 14.1 g/m^2 between May 30 and June 29. Walker found a biomass decline after peak of 4.25 g/m^2/day in the poorly drained site, and 8.31 g/m^2/day in the better drained site. Pickett's daily production rates for *Peltandra* ranged from -0.8 g/m^2/day on July 8 to 1.4 g/m^2/day on June 2. Doumlele (1981) found *Peltandra* produced at the highest rates early in the growing season, May to June, with 1.42 g/m^2/day, which was lower than the peak value in the present study.

Pickett (1984) calculated mortality rate constants for *Peltandra* that ranged from 2.2 to 2.9% per day from June to August 1982 and 1.5 to 1.7% per day from May to July 1983, in contrast to 0.07% to 11.57% per day found in this study. Whigham et al. (1978) refer to an unpublished study by Whigham and Simpson that measured leaf mortality in a 55 day tagging study for *Bidens*, *Acorus*, *Peltandra*, and *Sagittaria*. The leaf mortality over the 55 days ranged from 61.3% to 77%; *Peltandra* had a 66% mortality, with a 1.2% per day leaf mortality rate.

Life spans were short compared to salt marsh grasses and sedge wetlands. Bernard and Gorham (1978) reported a range of 1.5 to 2 years for the maximum life span of *Carex rostrata*. Bernard (1975) found that *Carex lacustris* shoots live for about 12 to 14 months; however, a group of shoots that emerged in late July or August died in late autumn, having lived only 2 to 3 months. Shew et al. (1981) found a mean longevity for *Spartina alterniflora* of 7.9 months in a North Carolina wetland. Longevity for fleshy emergents has not been studied extensively, although Hopkinson et al. (1978) reported that *Sagittaria falcata* leaves grow and die rapidly. Whigham et al. (1978) and Pickett (1984) suggest that *Peltandra* shoots have a rapid turnover, but did not determine longevity of individuals.

Turnover

Turnover traditionally has been calculated by dividing NAAP by peak biomass or mean biomass (Gosselink et al., 1977). The NAAP in these calculations typically has been estimated from multiple harvests. Recently estimates of mortality have been included and higher turnover rates have been found (Bernard and Hankinson, 1979; Shew et al., 1981; Dickerman et al., 1986). Pickett's (1984) turnover for *Peltandra* calculated from the ratio of the peak standing crop to the mortality NAAP estimate was 2.87. This study calculated a turnover of 2.24. The mean life span of plants from this study was short and thus the turnover rate based on longevity was high, since, when longevity decreases turnover increases (Odum, 1971). Hopkinson et al. (1980) calculated a

9.1 turnover for _Sagittaria_ _falcata_ that was based on longevity and the ratio of growth to average standing stock. Westlake (1971) (from Bernard and Hankinson) found a turnover of 1.5 to 3.0 for _Glyceria maxima_ when mortality was included in the NAAP. Turner (1976) found that turnover decreases with increasing latitude, so turnover estimates in higher latitudes may not be as important as they are in lower latitudes. The turnover estimated from the ratio of NAAP (from mortality) to peak biomass was smaller than the longevity based turnover and the ratio of NAAP to mean biomass. Shew et al. (1981) suggest that the turnover based on longevity is the most accurate since it is independent of any production estimate.

CONCLUSIONS

The estimates of net annual aboveground production as determined by the mortality and Allen curve methods are more accurate than the peak biomass or Smalley methods. Tagging methods account for seasonal mortality, recruitment, and turnover of each shoot that was produced in permanent plots. The peak biomass and Smalley methods result in underestimates because they do not account for mortality, turnover, or production between sampling intervals. The findings of high ongoing mortality and recruitment and a short life span support the differences found between tagging and harvest studies. The most accurate estimates of production, especially for species with high turnover and mortality, should include detailed observations of life history and population parameters. However, when detailed tagging studies cannot be conducted because of cost or time restrictions, species and latitude specific turnover rates should be applied to changes in harvested biomass measurements (Turner, 1976; and Dickerman et al., 1986). Harvested biomass values can be corrected for turnover by using literature derived turnover and leaf mortality rates. These values must be species and latitude specific because of production and turnover variation between species and location (Dickerman et al., 1986).

APPENDIX I

DESCRIPTION OF METHODS

A. <u>Peak Biomass Method</u>

1. Ten monthly harvests were made throughout the growing season.
2. The maximum live standing crop harvested was used as the estimate of NAAP.

B. <u>Smalley's Method</u>

Production was estimated from the sum of the positive changes in live and dead biomass for each month. NAAP was calculated as follows:

1. If the net change between sampling periods was positive for both live and dead, then production was their sum.
2. If the change in live and dead were negative, production was assumed to be zero.
3. If the change in live was positive and the change in dead was negative, production was equal to the change in live.
4. If the change in live was negative and the change in dead positive, production was their sum, if the sum was greater than zero, and equal to zero if the sum was negative.

C. <u>Mortality Method</u>

In eight 0.25 m^2 permanent plots all shoots were tagged every two weeks throughout the growing season. Tagging was done by writing identification numbers with permanent ink on the upper surface of the leaves.

Steps 1 - 6 were done for each 0.25 m^2 plot.

1. All shoot data were sorted by tag number.
2. Maximum size class reached by each shoot was recorded on the date of death. Date of death was the tagging date after the last measurement.
3. The number that died in each size class for each date was recorded.
4. Mean size class weights from harvest data were applied to the corresponding height classes.
5. The weights for each size class were multiplied by the number of shoots in each the class.
6. A total weight of shoot biomass lost for each date was calculated by summing the weights from all size classes.
7. A mean mortality from the eight plots was calculated for each date.
8. Mean mortality was summed over all dates resulting in the NAAP estimate.
9. The peak biomass of spathes and stipules was added to the result from step 8 for the final mortality NAAP.

D. Allen Curve Method

1. All tagged shoots in each plot were sorted by tag number.
2. Shoots were sorted by cohort, a cohort was defined as those shoots initially tagged on the same date.

The following steps were done for each cohort individually.

3. The size class measured on each date for each shoot was recorded.
4. For each tag date the number of shoots in each size class was recorded.
5. Size class weights from harvested shoots were applied to the corresponding height classes.
6. A mean weight for each date was calculated.
7. Allen Curves were made for each cohort with shoot mean dry weight on the abscissa and number of shoots on the ordinate.
8. Cohort production was proportional to the area below the curve.
9. Production for a plot was the sum all cohorts.
10. NAAP was estimated as the mean from the eight tagged plots.
11. The peak biomass of spathes and stipules was added to the result of step 10 for the final Allen curve NAAP estimate.

LITERATURE CITED

Allen, K. R. 1951. The Horokiwi Stream: a study of a trout population. Fisheries Bulletin of Wellington, New Zealand 10:1-238.

Bernard, J.M. 1975. The life history of shoots of *Carex lacustris*. Canad. J. of Bot. 53:256-260.

Bernard, J. M., M. L.and Fitz. 1979. Seasonal changes in aboveground primary production and nutrient contents in a central New York *Typha glauca* ecosystem. Bull. Torrey Bot. Club 106:37-40.

Bernard, J. M., and G. Hankinson. 1979. Seasonal changes in standing crop, primary production and nutrient levels in a *Carex rostrata* wetland. Oikos 32:328-336.

Bernard, J. M., and E. Gorham. 1978. Life history aspects of primary production in sedge wetlands. In: R. E. Good, D. F. Whigham, and R. L. Simpson (eds). Freshwater Wetlands Ecological Processes and Management Potential. p. 39-51. Academic Press, New York.

Bernard, J. M., and J. G. MacDonald, Jr. 1973. Primary production and life history of *Carex lacustris.* Can. J. Bot. 52:117-123.

Booth, P. M. 1989. (in press) Nitrogen and phosphorus cycling in two tidal freshwater macrophytes, *Peltandra virginica* and *Spartina cynosuroides*. Ph.D. dissertation, Virginia Institute of Marine Science, College of William and Mary, Williamsburg, VA

de la Cruz, A. A. 1978. Primary production processes: summary and recommendations. In: R. E. Good, D. F. Whigham, and R. L. Simpson (eds). Freshwater Wetlands: Ecological Processes and Management Potential. p. 79-86. Academic Press, New York.

Doumlele, D.G. 1981. Primary production and seasonal aspects of emergent plants in a tidal freshwater marsh. Estuaries 4:139-142.

Dickerman, J. A., A. J. Stewart, and R. G. Wetzel. 1986. Estimates of net annual aboveground production: sensitivity to sampling frequency. Ecology 67:650-659.

Gallagher, J. L., R. Reimold, R. Linthurst, and W. Pfeiffer. 1980. Aerial production, mortality, and mineral accumulation-export dynamics in Spartina alterniflora and Juncus roemerianus plant stands in a Georgia salt marsh. Ecology 61:303-312.

Giroux, J. and J. Bedard. 1988. Estimating above- and below-ground macrophyte production in Scirpus tidal marshes. Can. J. Bot. 66:368-374.

Goldberg, B. 1941. Life history of Peltandra virginica. The Botanical Gazette 102(4)641-661.

Gosselink, J. G., C. S. Hopkinson, and R. T. Parrondo. 1977. Minor marsh plant species. Vol. I. Production of marsh vegetation. Final report to dredged material research program. U.S.A.E.C., Waterways Experiment Station, Vicksburg. Mississippi.

Grant, R. R., and R. Patrick. 1970. Tinicum marsh as a water purifier. In: Two studies of Tinicum marsh, p. 105-123. The Conservation Foundation, Washington, D.C.

Hardisky, M. A. 1980. A comparison of Spartina alterniflora primary production estimated by destructive and nondestructive techniques. In: V. S. Kennedy (ed.) Estuarine Perspectives, Academic Press, NY. p. 223-234.

Hardisky, M. A. and R. J. Reimold. 1977. Salt-marsh plant geratology. Science 198:612-614.

Hopkinson, C. S., J. G. Gosselink, and R. T. Parrondo. 1978. Aboveground production of seven marsh plant species in coastal Louisiana. Ecology 59:760-769.

Hopkinson, C. S., J. G. Gosselink, and R. T. Parrondo. 1980. Production of coastal Louisiana marsh plants calculated from phenometric techniques. Ecology 61:1091-1096.

Houghton, R. A. 1985. The effect of mortality on estimates of net above-ground production by Spartina alterniflora. Aquatic Botany 22:121-132.

Linthurst, R. A., and R. J. Reimold. 1978. An evaluation of methods for estimating the net aerial primary productivity of estuarine angiosperms. Journal of Applied Ecology 15:919-931.

Lomnicke, A., E. Bandola, and K. Jankowska. 1968. Modification of the Wiegert-Evans method for estimation of net primary production. Ecology 49:147-149.

Mason, C. F., and R. J. Bryant. 1975. Production, nutrient content and decomposition of Phragmites cummunis Trin. and Typha angustifolia L.. Journal of Ecology 63:71-95.

Mathews, C. P., and D. F. Westlake. 1969. Estimation of production by populations of higher plants subject to high mortality. Oikos 20:156-160.

McCormick, J. and H.A. Somes, Jr. 1982. The coastal wetlands of Maryland. Jack McCormick and Associates, Inc. Chevy Chase, Maryland. 241 pp.

Milner, C., and R. E. Hughes. 1968. Methods for the Measurement of the Primary Production of Grassland. IBP Handbook No. 6. Blackwell Scientific Publications, Oxford, England. 70 pp.

Mitsch, W. J., and J. G. Gossilink. 1986. Wetlands. Van Nostrand Reinhold Co. Inc. 537 p.

Odum, E. P. 1971. Fundamentals of Ecology. W. B. Saunders Co., Philadelphia. 574 p.

Odum, W. E., and M. A. Heywood. 1978. Decomposition of intertidal freshwater marsh plants. In: R. E. Good, D. F. Whigham, and R. L. Simpson (eds.) Freshwater Wetlands Ecological Processes and Management Potential. p. 89-97. Academic Press, NY.

Odum, W. E., M. L. Dunn, and T. J. Smith. 1979. Habitat value of tidal freshwater wetlands. In: P. E. Greeson, J. R. Clark and J. E. Clark, (eds.) Wetland Functions and Values: the State of Our Understanding. Proc. National Symposium on Wetlands, American Water Resources Association, Minneapolis, MN. p. 248-255.

Odum, W. E., T. J. Smith III, J. K. Hoover, and C. C. McIvor. 1984. The ecology of the tidal freshwater marshes of the U. S. East coast: a community profile. U. S. Fish. Wild. Ser. FWS/OBS-83/17. 177 pp.

Pickett, J. R. 1984. Community composition and net primary production of emergent macrophytes in a South Carolina tidal freshwater marsh ecosystem. Thesis, Univ. of South Carolina, Columbia, South Carolina. 54 pp.

Reidenbaugh, T. G. 1983. Productivity of cordgrass, Spartina alterniflora, estimated from live standing crops, mortality and leaf shedding in a Virginia marsh. Estuaries 6:57-65.

Robb, D. L. 1968. Transplant experiments and toxicity tests in Peltandra. Canadian Field Naturalist 82:225-226.

Shew, D. M., R. A. Linthurst, and E. D. Seneca. 1981. Comparison of production computation methods in a southeastern North Carolina Spartina alterniflora salt marsh. Estuaries 4:97-109.

Simpson, R. L., R. E. Good, M. A. Leck and D. F. Whigham. 1983. The ecology of freshwater tidal wetlands. Bioscience 33:255-259.

Smalley, A. E. 1958. The role of two invertebrate populations, *Littorina irrorata* and *Orchelimum fidicinium* in the energy flow of a salt marsh ecosystem. Dissertation. Univ. of Georgia, Athens, Georgia. 126 pp.

Smith, L. M., and J. A. Kadlec. 1985. A comparison of marsh plant loss estimates in production techniques. American Midland Naturalist 114:393-395.

Turner, R. E. 1976. Geographic variations in salt marsh macrophyte production: A review. Contrib. in Marine Sci. 20:47-67.

Walker, R. 1981. Nitrogen, phosphorus and production dynamics for *Peltandra virginica* (L.) Kunth in a southern New Jersey freshwater tidal marsh. Ph.D. Dissertation, Rutgers University, New Brunswick, NJ.

Weigert, R. G., and F. C. Evans. 1964. Primary production and the disappearance of dead vegetation on an old field in southeast Michigan. Ecology 45:49-63.

Westlake, D. F. 1971. Population dynamics of *Glyceria maxima*. Hydrobiologia 12:133-134.

Whigham, D. F., J. McCormick, R. E. Good, R. L. Simpson. 1978. Biomass and primary production in freshwater tidal wetlands of the middle Atlantic coast. In: R. E. Good, D. F. Whigham, and R. L. Simpson (eds.) Freshwater Wetlands Ecological Processes and Management Potential. Academic Press, NY. p. 3-20.

Whigham, D. F., and R. L. Simpson. 1975. Ecological studies of the Hamilton Marshes. Progress report for the period June 1974-January 1975. Rider College, Biology Department, Lawrenceville, NJ. 185p.

Williams, R. B., and M. B. Murdoch. 1972. Compartmental analysis of the production of *Juncus roemerianus* in a North Carolina salt marsh. Chesapeake Sci. 13:69-79.

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